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EFFECT OF TEMPERATURE ON GERMINATION OF AMARANTHUS RETROFLEXUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 291

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(WITH FOUR FIGURES)

Introduction

The literature having a direct bearing on the effect of temperature on germination may be divided into two groups: one deals with growth in relation to temperature, and the other with delay in germination of seeds in general and of *Amaranthus retroflexus* in particular. In the first group the articles by SMITH (10), LEHENBAUER (7), LEITCH (8), BALLS (1), and KANITZ (6) on relation of growth to temperature are of interest. SMITH found that temperature, possibly internal temperature of the growing parts, may be a limiting factor to growth in *Furchraea* and *Agave*. LEHENBAUER, in his work on rate of growth of maize seedlings, found that the Van't Hoff law applies only at medium temperatures; at 31° C. the initial rate is not maintained, there being a falling off with time. He further found that the coefficients for 10° C. rise in temperature are greater at lower ranges of temperature (6.56 at 12°–22° C.), and less (0.06 at 33°–43° C.) at higher ones. He states that the optimum changes with length of exposure, and that there are not two optima, as stated by KOEPPEN. Miss LEITCH, in work with rate of growth of seedlings of *Pisum sativum*, found that the Van't Hoff law applies only from 10° to 28° or 30° C.; that there is the same type of gradation in the coefficients relating rate of growth to temperature that LEHENBAUER found; and that above 29° C. the relation of growth to temperature can no longer be expressed as a curve, so that a different curve must be constructed to express the rate of growth in successive time intervals. She defined the optimum temperature as the highest one at which the time factor does not enter. BALLS offers an explanation of the time factor, and says

that the Van't Hoff law applies approximately up to 30° C., then the growth rate acceleration decreases to a point which he proposes to call the "stopping point," a point below the lethal temperature.

KANITZ has written a monograph on the effect of temperature of life processes in which he cites over three hundred pieces of literature distributed among several fields. The following is based on DENNY'S review of this monograph. He derives formulae from those of BERTHELOT, ARRHENIUS, VON ESSEN, and VAN'T HOFF, by means of which the value of Q_{10} , the coefficient for 10° C. rise in temperature, can be calculated from experimental data at any two temperatures. These formulae are $Q_{10} = \left(\frac{k_2}{k_1}\right)^{\frac{10}{t_2-t_1}}$ and $Q_{10} = \frac{10(\log k_2 - \log k_1)}{t_2 - t_1}$, in which k_2 =rate of process at temperature t_2 , and k_1 =rate of process at temperature t_1 . He found that when he calculated results at short temperature intervals instead of long ones, Q_{10} is often not a constant at all intervals, but falls at high temperatures. He also states that many processes in plants and animals exhibit a temperature coefficient the same as the Van't Hoff one within certain temperature limits, and cites in this connection such plant processes as CO_2 assimilation between 0° and 37° C. (MATTHAEI); respiration of seedlings between 0° and 35° C. (KUIJPER); water intake of barley grains between 3.8° and 34.6° C. (BROWN and WORLEY); permeability of plant cells and tissues between 0° and 30° C. (RYSSELBERGHE); etc. Some of these processes show higher values of Q_{10} at lower temperatures, or temperatures near the minimum of the process.

BEAL (2) has found that seeds of *Amaranthus retroflexus* are long lived; that they are still viable after burial in the ground for thirty years. Delays in germination of seeds are due (putting aside the stimulus idea held by some workers) either to embryo characters such as immaturity of embryo, or need of fundamental chemical changes in the embryo preceding germination in a seemingly otherwise mature embryo (5), or to coat effects acting jointly with embryo characters. The embryo in the latter case is not dormant when naked and exposed to ordinary germinative conditions.

These coat effects may be of several kinds, namely, the almost complete exclusion of water from the embryo, as in some Leguminosae, the cutting down of oxygen supply below the minimum required for germination (9), or the high elasticity or breaking strength of the coats as compared with the force of the expanding embryo (3, 4).

CROCKER (3) and CROCKER and DAVIS (4) state that this last named coat effect is the chief cause of dormancy in seeds of *Amaranthus retroflexus*. This dormancy gradually disappears in dry storage, as is shown by a continual lowering of the minimum temperature for germination. On the other hand, wild oats, "rain barley," and a South American grass, *Chloris ciliata*, have a low maximum when not after-ripened, which rises as after-ripening progresses. Even in seeds of *Amaranthus retroflexus* which have been stored for a long time, incompleteness of after-ripening is indicated by the considerable lingering effects of the coats. Fully after-ripened seeds have their minimum for germination lowered by removal of coat restrictions. In fresh *A. retroflexus* seeds with coats treated, the minimum temperature for germination is the same as in dried seeds with coats treated. Vigor of the embryo of *A. retroflexus*, ability to respond in germinative conditions, and the rate of growth of the naked embryo under any given conditions is not affected noticeably by after-ripening. In this seed after-ripening seemingly is not a matter of after-ripening of the embryo, for embryos of fresh seed are of maximum vigor if coat effects are removed. That the breaking strength of these coats is lowered by a rise in temperature is shown by the fact that ripe seeds gathered from green plants will not germinate at temperatures lower than 40° C., but will germinate slightly at that temperature. *A. retroflexus* seeds are slightly inhibited by light at all temperatures, according to the unpublished experiments of CROCKER and DAVIS. This holds for seeds in which the coats are treated as well. Knowledge of these conditions was requisite to handling the material intelligently in finding the series of coefficients relating rate of germination of *A. retroflexus* to temperature changes.

Material and method

Three lots of seeds were used: one gathered in late summer or early fall, 1915, at Pullman, Washington; and the other two at Gary, Indiana, one lot in the late summer or early fall of 1914, and the other a year later. The experiments extended from March 15 to August 1, 1916. Thus after-ripening had proceeded for several months in two lots, and for one year and several months in the third lot. In some of the experiments, remaining coat effects were further eliminated by grinding some of the seeds with sand for four, six, or nine weeks, or treating them with concentrated H_2SO_4 for two or three minutes and then washing them with running tap water for two minutes. The optimum length of time for treatment with H_2SO_4 was determined by experiment to be two minutes for Indiana seeds, and three minutes for Washington seeds. Along with these treated seeds were run seeds with coats not treated. These seeds, treated and untreated, were then put in lots of one hundred in Petri dishes lined with moist absorbent cotton. The Petri dishes were placed in a cardboard box lined with opaque black paper, and the box then put in a refrigerator for forty-eight hours, where the temperature was below the minimum necessary for germination, to allow time for the seeds to soak before they were tested for temperature effects on rate of germination. At the end of this time the box containing the Petri dishes was kept at the desired constant temperature. The temperatures tested ranged from 9° to 42° C. Temperatures below room temperature were obtained in baths cooled with running water, and at room temperature and above, in a constant temperature incubator in which the variation was less than one degree. At one time only did the temperature vary more than this, and then it was in the water-cooled bath; this variation is indicated on the curves 1, 2, and 3, and in all the tables thus, (8° – 10° C.).

The percentage germination at various intervals of time for each temperature tried was noted for all seeds in the box. The results were plotted as curves; one set of curves for each type of seeds, that is, one set of curves for Indiana seeds collected in 1915 and treated with H_2SO_4 for two minutes, another set for Indiana seeds collected in 1915 and ground with sand nine weeks, another

set for Indiana seeds collected in 1915 and untreated, another for Washington seeds untreated, etc. Eleven sets of curves were thus plotted, three of which are included in this paper as fairly typical ones. Not fewer than two hundred seeds of each type were germinated at each temperature, one hundred each in a separate Petri dish, so that all determinations were made at least in duplicate. In some instances four hundred seeds of each type were used, making quadruplicate determinations.

From these curves, three sets of which are given as typical, the length of time required for certain percentage germination at two different temperatures was read, and these readings and temperatures used in the KANITZ formula: $Q_{10} = \left(\frac{k_2}{k_1} \right)^{\frac{10}{t_2 - t_1}}$, in which k_2 = rate of germination at temperature t_2 , and k_1 = rate of germination at temperature t_1 . The rate of germination in each case of course was the percentage germination divided by the number of hours required for this to take place. The results of these computations are given in tables I to XI.

Again similar experiments were run and attempts made to secure lots of seeds at the same percentage germination with hypocotyls the same length when the seeds were subjected to different temperatures. These readings were used exactly as were the ones from the curves previously mentioned, and as they gave the same type of coefficients, for the sake of brevity are omitted here.

TABLE I

INDIANA SEEDS, COLLECTED 1915, UNTREATED

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*									
	12	14	20	28	30	40	50	60	70	80
11.9-16.3.....	11.69	12.14	11.91	17.6
16.3-25.3.....	2.95	3.05	2.94	2.87	3.68	4.01
25.3-36.4.....	1.71	1.76	1.83	1.85	1.89	2.01	2.06	2.04	2.21
36.4-42.....	1.14	1.13	Less than 1	Less than 1	Less than 1	1.14	1.28	1.49	1.37
16.3-36.4.....	2.19	2.25	2.25	2.55	2.74
23.9-36.4.....	1.68	1.72	2.11	2.02	2.29	2.41	2.96	2.94	3.53

* No germination at 8°-10° in 168 hours.

TABLE II

INDIANA SEEDS, COLLECTED 1915, GROUND WITH SAND NINE WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*									
	12	14	20	30	36	40	50	60	70	80
(8 to 10)-16.3....	10.01	8.34
16.3-21.6.....	4.43	4.33
21.6-29.8.....	1.20	1.31	1.30	1.30	1.32	1.36	1.45	1.44
29.8-42.....	1.677	1.641
16.3-23.9.....	3.65	3.55	3.42	3.27	3.13	2.88
23.9-42.....	1.27	1.29	1.27	1.29	1.33	1.32

* 15 per cent germination at 8°-10° in 156 hours.

TABLE III

INDIANA SEEDS, COLLECTED 1915, TREATED WITH H₂SO₄ TWO MINUTES

Temperature interval (° C.)	Q ₁₀ at certain percentage germination							
	20	30	40	50	60	70	75	80
(8 to 10)-11.9...	1.778	2.118	5.91
11.9-14.45....	7.48	6.16	5.22	6.97	10.44	12.36	28.73
14.45-23.4....	3.69	3.81	3.82	3.83	3.66	3.70	3.74	4.27
23.4-36.4....	1.999	1.89	1.95	1.89	1.96	1.87	1.95	2.07
36.4-42.....	1.93	1.74	1.45	1.32	1.23	1.27	1.25	1.161
14.45-28.9....	2.81	2.92	2.73	2.39	2.18	1.76
21.6-28.9....	1.53	1.89	1.88	1.74	1.57	1.497	1.903
14.45-36.4....	2.63	2.53	2.57	2.53	2.53	2.49

TABLE IV

INDIANA SEEDS, COLLECTED 1915, GROUND WITH SAND FOUR WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination									
	4	8	10	20	30	40	50	64	70	80
(8 to 10)-23.9.....	4.82	4.74
16.3-23.9.....	2.33	2.50	2.91
23.9-36.4.....	1.61	1.60	1.90	1.87	1.91	1.93	1.86	1.88	1.84	1.94
36.4-42.....	1.28	1.24	1.25	1.13	1.02	1.10	1.09
(8 to 10)-21.6.....	5.75	6.05
23.9-29.8.....	2.79	1.93	1.91	1.83	1.75	1.22	1.65

TABLE V

WASHINGTON SEEDS, COLLECTED 1915, UNTREATED

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*				
	2	8	10	12	15
11.9 -14.45.....	8.173	10.32	11.75	5.1
14.45-25.7.....	2.40	2.37	2.89
25.7 -36.....	1.40	1.33	1.38
36 -42.....	0.1928
23.9 -36.....	1.15	1.11	1.17
14.45-36.....	2.57	1.86	1.79	1.83

* No germination at 8°-10° in 168 hours.

TABLE VI

WASHINGTON SEEDS, COLLECTED 1915, TREATED WITH H₂SO₄ THREE MINUTES

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*					
	10	20	30	40	50	58
11.9 -14.45.....	5.77	5.77	5.66	5.15	1.86	1.0
14.45-23.4.....	3.82	3.40	3.30	4.05	4.52	5.17
23.4 -36.4.....	1.95	1.84	1.70	1.57	1.52	1.47
36.4 -42.....	2.36	1.37	1.21	1.21	1.13	1.08
21.6 -29.8.....	1.72	2.26	2.20	2.03
14.45-36.4.....	2.55	2.36	2.21	2.14	2.33
14.45-29.8.....	2.56	2.32	1.98	1.60

* Only 2 per cent germination at 8°-10° in 84 hours.

TABLE VII

WASHINGTON SEEDS, COLLECTED 1915, GROUND WITH SAND FOUR WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*						
	16	20	30	36	40	50	54
11.9 -14.45.....	9.07	8.84	8.09	6.74
14.45-25.7.....	3.05
25.7 -37.6.....	1.18	1.59	1.75	1.91
14.45-37.6.....	2.16	2.10	2.03	2.026

* 8 per cent germination 8°-10° in 156 hours.

TABLE VIII

WASHINGTON SEEDS, COLLECTED 1915, GROUND WITH SAND SIX WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*						
	10	20	30	40	50	60	70
16.3-23.4.....	2.28	2.10	2.05
23.4-42.....	1.45	1.36	1.24
16.3-21.6.....	2.62	2.80	2.58	2.67	2.34	2.29
21.6-29.8.....	2.38	2.07	2.25	2.21	2.37	2.60
16.3-29.8.....	2.48	2.32	2.37	2.38	2.35	2.47	2.65
29.8-42.....	0.715	0.5799

* No germination at 8°-10° after 168 hours, and temperatures between this and 16.3° not tried.

TABLE IX

WASHINGTON SEEDS, COLLECTED 1915, GROUND WITH SAND NINE WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*				
	10	15	20	22	30
16.3-21.6.....	2.29	2.33	2.79
16.3-23.9.....	1.99	1.74	1.48	1.44
23.9-42.....	1.65	1.79	1.85
16.3-29.8.....	2.53	2.54	2.95
21.6-29.8.....	2.68	2.64	3.06

* No germination at 8°-10° after 168 hours, and temperatures between this and 16.3° not tried.

TABLE X

INDIANA SEEDS, COLLECTED 1914, UNTREATED

Temperature interval (° C.)	Q ₁₀ at certain percentage germination						
	12.5	15	20	30	40	50	60
11.9-14.45....	12.82	9.60	13.15	16.85
14.45-23.9....	3.92	4.37	4.50	4.62	4.47
23.9-42.....	1.54	1.55	1.55	1.42
14.45-42.....	2.42	2.23

TABLE XI

INDIANA SEEDS, COLLECTED 1914, GROUND WITH SAND TWO WEEKS

Temperature interval (° C.)	Q ₁₀ at certain percentage germination*						
	22	30	40	50	60	70	80
11.9-14.45.....	8.75	8.88	8.30	8.001	6.65	11.42
14.45-23.4.....	3.58	3.58	3.84	4.19	4.54	4.91	5.40
23.4-36.4.....	1.92	1.91	1.89	1.89	1.92	1.88	1.68
36.4-42.....	1.24	1.22	1.18	1.10	1.06	1.35
14.45-29.8.....	2.91	3.03	3.24	3.41	3.72	3.94	4.35
23.4-29.8.....	1.93	1.97	2.14	2.09	2.12
14.45-36.4.....	2.44	2.48	2.53	2.61	2.75	2.79	2.72

* 5 per cent germination at 8°-10° in 168 hours.

Discussion

In the effort to find a representative end point, many different ones were tried, with the result that almost any one proved satisfactory. These end points are Q_{10} at different percentage germination. A study of the tables shows that almost any percentage germination up to the total at the temperature might well serve for this representative end point, as in practically every series the coefficient for 10° C. rise in temperature is more than three when computed at temperature intervals near the minimum temperature for germination, and gradually decreases to about one or even less than one near the maximum. At some range between these, of course, Q_{10} falls between two and three. It is interesting that by computing through a long temperature interval Q_{10} may be found to be between two and three, when computations over shorter intervals of this longer one show Q_{10} not a constant but a variable. Take, for instance, from table III Q_{10} at the range of temperature 14.45°-36.4° = 2+, while Q_{10} at 14.45°-23.4° = 3.6 to 4+, 23.4°-36.4° = 1.8 to 2.0. Here Q_{10} , computed through a long interval where its values range from 4 to 1.8, gives an average value of 2+. This is the sort of thing to which KANITZ called attention. The series of coefficients computed through short temperature intervals agrees in general type with those given by LEITCH for effect of temperature on rate of growth of seedlings of *Pisum sativum*, with those given by LEHENBAUER for rate of growth of corn seedlings in

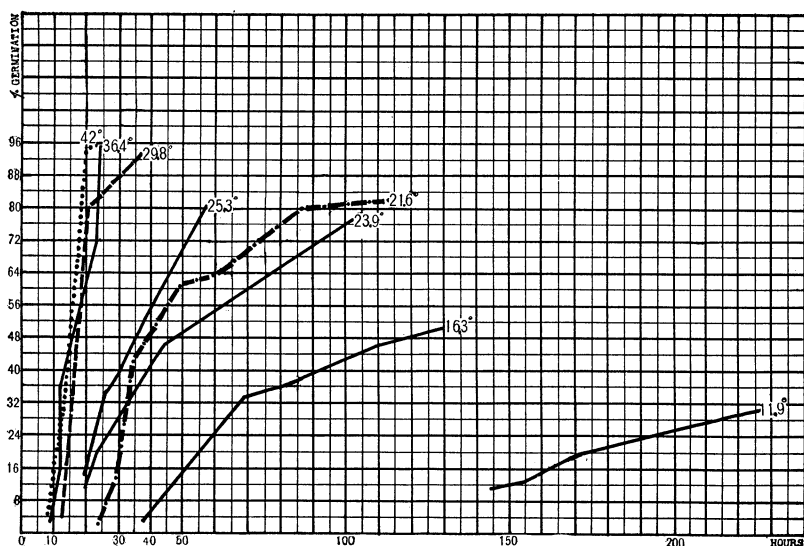


FIG. 1.—Rate of germination at certain temperatures (° C.) of seeds of *Amaranthus retroflexus*, collected at Gary, Indiana, in 1915, and untreated.

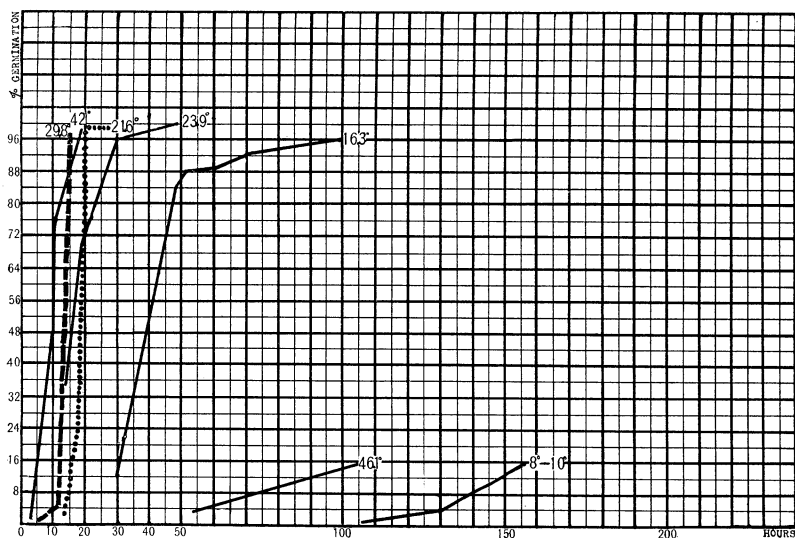


FIG. 2.—Rate of germination at certain temperatures (° C.) of seeds of *Amaranthus retroflexus* collected at Gary, Indiana, in 1915, and ground with sand nine weeks before being set to germinate.



FIG. 3.—Rate of germination at certain temperatures ($^{\circ}$ C.) of seeds of *Amaranthus retroflexus* collected at Gary, Indiana, in 1915, and treated with concentrated H_2SO_4 two minutes before being set to germinate.

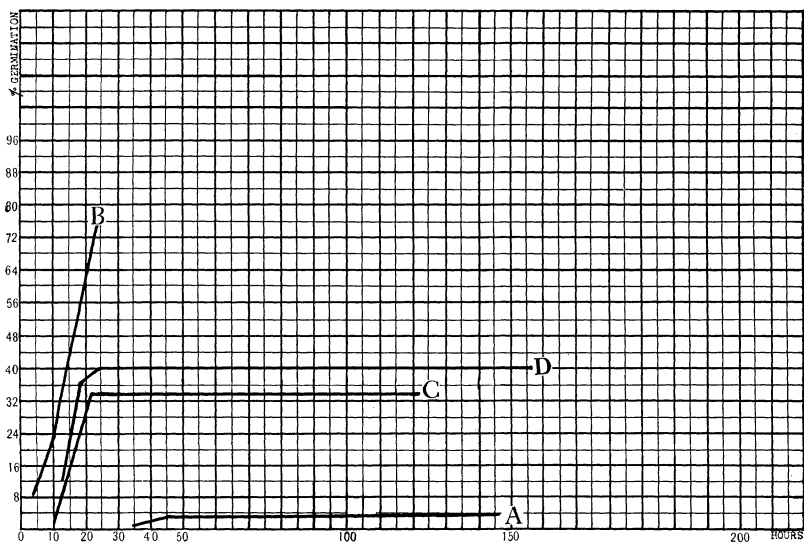


FIG. 4.—Relative rate and total percentage germination at 42° C. of *Amaranthus retroflexus* seeds collected at Pullman, Washington, in 1915: (A) untreated before being set to germinate; (B) treated with concentrated H_2SO_4 ; (C) ground with sand six weeks; (D) ground with sand nine weeks.

relation to temperature, and with those given by BALLS for rate of growth of sore-shin fungus in relation to temperature. Omissions in the tables of coefficients are due to lack of comparative data at certain temperatures.

Figs. 1, 2, and 3, included as representative graphs, show the difference in total percentage germination of seeds collected at the same time in one locality, and germinated at the same time at the same temperature but with seed coat intact in one lot, abraded by grinding with sand in another, and carbonized with H_2SO_4 in the third lot. This difference in total germination is greatest at low temperatures. Nevertheless, the coefficients for rate of germination computed from these curves in all lots run remarkably similar (tables I-III).

Fig. 4 shows the striking restricting effect of the coat at high temperatures, an effect paralleling the magnitude of the restricting effect of this coat at temperatures near the minimum temperature for germination. The removal of coat effects, either by grinding the seeds with sand or by treating with H_2SO_4 , allows much more rapid germination at the same high temperature ($42^\circ C.$) for the Washington seeds. Effects somewhat paralleling these were obtained for Indiana seeds at $46.1^\circ C.$ In fig. 4 the effect of grinding the seeds with sand nine weeks is shown to be greater than the effect of grinding for six weeks. Concomitant with this slowness in germinating is the lack of anthocyanin in the seedlings developed at these high temperatures, and again apparently lessened amount in the seedlings developed at the lowest temperatures at which germination took place at all.

Conclusions

1. The coefficients relating rate of germination of seeds of *Amaranthus retroflexus* to temperature grade from high values as 10.01 (table II) at low temperatures, to low values as 0.001 (table II) at high temperatures, thus paralleling the coefficients relating rate of growth of seedlings and sore-shin fungus to temperature worked out by LEITCH, LEHENBAUER, and BALLS.

2. The general trend of these coefficients is the same for seeds only partially after-ripened, and for those with coat effects almost

completely removed by treatment with H_2SO_4 or abrasion with sand, as for instance 11.75 to 1.33 for Washington seeds untreated, and 5.77 to 1.37 for these seeds when treated with H_2SO_4 for three minutes.

3. In after-ripened seeds with coats untreated, the restricting effect of the coats shows particularly at low temperatures 8° – 10° and 11.6° , and again at high temperatures, 42° for Washington seeds, and 46.1° for Indiana seeds. In both cases these effects can be lessened by treating the coats with H_2SO_4 or abrading them with sand.

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